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The roles of competition and climate in tree growth variation in northern boreal old-growth forests

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Abstract

Questions How have tree growth and growth trends varied in structurally complex old-growth forests? What determines this variation, and how this differs among species?

Location Naturally developed boreal old-growth forests at high latitudes in northern Finland

Methods We sampled trees over 10 cm diameter on 48 randomly located 0.1 ha plots in three landscapes, and compiled a dataset of 1565 trees including all three main species, and a full range of sizes and competitive states in northern boreal old-growth forests. We extracted tree ring samples from every tree, and used ring widths to reconstruct tree sizes and their neighborhood for the past 50 years for *Pinus sylvestris* and *Picea abies*, and 30 years for *Betula pubescens*. We used mixed-effects models to study variation in tree growth. In the models, we used annually varying environmental variables, forest and tree structural variables and site variables as predictors. We also measured soil hydraulic properties for a water balance model to specifically include soil moisture deficits as predictors.

Results Tree growth rates had increased during the analysis period for all three species, with the highest increases for *P. sylvestris* and *B. pubescens*. All three species grew well during warm summers, but *P. sylvestris* and *P. abies* growth was also negatively influenced by soil moisture deficits. Competition in these sparse forests had a small influence on growth. However, its influence increased over time.

Conclusions The trees showed positive growth trends, but the increasing competition means that such strong positive trends are unlikely to continue over the long-term. For year-to-year variability, negative influence of droughts implied that increasing temperatures are not only beneficial to tree growth even in these high latitude forests. Overall, the findings demonstrate the site- and species-dependent complexity in tree responses to environmental and structural changes we may expect in the future.

Keywords: Drought; Tree ring; Picea abies; Pinus sylvestris; Betula pubescens; Mixed-effects model; Forest dynamics; Natural forest

Introduction

Boreal forests cover large areas of northern Europe and, importantly, high latitudes encompass a sizeable share of Europe's remaining intact forest landscapes (Potapov et al. 2017). Predicting their future requires understanding the factors that influence the growth of different tree species. Earlier studies from different biomes have demonstrated immense variation in tree growth at multiple time scales, ranging from year-to-year variation to long term, trend-like changes (Bowman et al. 2013). Such variation at different time scales can be driven by a multitude of factors, including tree size, tree-tree interactions, and climatic variability (Coomes & Allen 2007; Gómez-Aparicio et al. 2011). However, in many respects the high latitude forests have characteristic features that set them apart from lower latitude forests, including low tree species diversity, a short growing season, low sun angles, and a sparse canopy cover. Hence, factors influencing tree growth are also likely to vary from those documented at lower latitudes (Fraver et al. 2014).

In general, tree growth in high latitude boreal forests is considered to be limited by the availability of energy, and thus they are expected to display a sensitive and positive response to warming climate (Bonan & Shugart 1989). However, research from Alaska and northern Europe has also shown that, depending on site and tree species, tree growth may also be limited by water availability (Kärenlampi 1972; Barber et al. 2000; Wilmking et al. 2004; Henttonen et al. 2014). Nevertheless, at larger scales and for different tree species the evidence on environmental determinants of growth variation remains somewhat fragmentary.

In addition to the environmental limitations of growth, i.e. temperature and water availability, another characteristic feature influencing tree growth in these forests is their tendency to have fairly open canopies. As this allows the trees to avoid competition through crown plasticity (Aakala et al. 2016), it would suggest a minor role of tree-tree competition. However, Fraver et al. (2014) showed that despite the generally sparse nature of canopies, competition seems to play a role as a determinant of tree growth variation. Understanding the role competition plays for different tree species would be important also because the climate response of trees has been shown to be dependent on competition (Bottero et al. 2017). In addition, in naturally-developed forests, the spatial structures and tree size distributions often exhibit a much wider range than managed forests. This means that research findings on tree-tree interactions from orderly-developed managed forests maybe poorly generalizable to structurally complex natural forests.

Past strategies for the statistical modeling of growth of individual trees have varied depending on the variable of interest. Growth as a function of tree size, neighborhood interactions, and/or species has commonly been studied as average growth over multi-year intervals (e.g., (Hartmann et al. 2009; Fraver et al. 2014), whereas high-frequency variation in growth is commonly the focus in dendroclimatological studies, in which case the influence of other variables, such as tree size or age is considered noise (Foster et al. 2016). Moreover, as highlighted by Nehrbass-Ahles et al. (2014), the sampling in those studies is often geared towards specific purposes, such as maximizing the climate signal, and only on selected tree species and hence the results are not easily generalizable and are not representative of tree growth in forested landscapes. However, both categories of data (environmental variables, tree and neighborhood characteristics) are crucial to understand the factors determining the tree growth dynamics (Bowman et al. 2013).

Here, we assessed the trends and variation in tree growth over the past 50 years in naturally developed, old-growth forests in northern Finland. We employed a randomized network of plots to develop an annual-resolution reconstruction of stand development using tree ring-derived data of tree growth and changing competitive neighborhood. Using these data, and a mixed-effects modeling framework based on the approach presented by Lapointe-Garant et al. (2010) we aimed to 1) quantify variation and trends in tree basal area increment over the past 50 years, and 2) attribute the trends and interannual growth variation to tree- and stand-level variables and environmental drivers, including the influence of competition on the climate response of trees.

Material and methods

Study areas

We collected field data in the summer 2012 from Värriö and Maltio strict nature reserves in northeastern Finland (**Fig. 1**). The reserves are characterized by a mosaic of open mires, forest stands on mineral soils, and treeless areas in the upper slopes of gently rolling mountains (fells). The main tree species in the region are *Pinus sylvestris*, *Picea abies*, and *Betula pubescens* (*B. pubescens* may in these forests be rarely be mixed with *Betula pendula*, but we did not separate the two here). Climate in this area is subcontinental, with cold winters and relatively warm summers. Mean annual temperature is -1°C. July, the warmest month, has a mean temperature of 13°C, whereas the coldest month, February, has an average temperature of -12°C. Annual precipitation is approx. 660 mm, of which half falls as snow. Soils consist of quaternary deposits and vary from thin soils on stony sites, to deeper soils in the valleys and consist of both sorted soils and moraines.

The reserves, established in 1981 (Värriö) and 1956 (Maltio) have never been logged. The main anthropogenic impact is from reindeer herding. Forest fires have historically been an important

disturbance in the region, mainly low-intensity surface fires (Aakala 2018). Fire frequencies have decreased considerably in the modern times, and fires are nowadays almost absent in these landscapes. Another major disturbance agent is the *B. pubescens* defoliator *Epirrita autumnata*. Damage due to these defoliators is commonly associated with high elevation 'birch zones', but during an outbreak they may also influence *B. pubescens* and *Salix* spp. populations in the forested areas at lower elevations. In northeastern Finland, the previous outbreak was in 1965-66 that resulted in considerable *B. pubescens* mortality (Pulliainen 1976).

Field data

We collected field data from 48 randomly located plots in the three study areas Hirvaskangas and Pommituskukkulat in Värriö Strict Nature Reseve and Hongikkovaara in Maltio Strict Nature Reserve, as described in Aakala et al. (2016). In short, a 2 km × 2 km square was lain on aerial photographs in each study area. This square was then divided into quadrants, and each quadrant was sub-divided into 31.6 m x 31.6 m cells (0.1 ha). We randomly selected four of these 0.1 ha cells within each quadrant as sampling sites (16 per study area, 48 plots total). The first two sites were located close together, after which a buffer of 100 m was used for all consecutive plots (i.e., a plot was rejected if it the center was located less than 100 m away from the center of a plot already measured). We considered all 48 plots as old-growth forests, with the ages of the oldest trees in each site ranging from approx. 180 years up to 570 years (Aakala 2018).

Within each plot, we mapped all live and dead trees with diameter at 1.3 m height (diameter at breast height, DBH) over 10 cm, using the FieldMap measuring system (IFER, Czech Republic) that is designed for mapping forest stands. The system combines an electronic compass and a laser rangefinder to a mapping software. For all trees, we recorded their species, DBH, and height. Following mapping, we took increment core samples from all the trees, using a standard 5.15 mm

145 increment borer. We cored live and standing dead trees and cut a wedge from down dead trees,
146 using a chainsaw.
147
148 For an approximation of soil characteristics for water balance modeling we extracted four soil
149 samples from each site, at 2 m distances from plot center to each cardinal direction. The samples
150 were extracted from the parent material a few cm below the B horizon. As it was not logistically
151 possible to analyze the influence small-scale (i.e., within-plot) variation, we pooled these four soil
152 samples, and determined an average particle size distribution from the oven-dried <2 mm soil
153 fraction using laser diffraction (Coulter LS 230, Beckman Coulter Inc.). Stoniness was similarly
154 determined as a single plot average value, using a metal probe at 16 locations around the plot center
155 (Viro 1952), four points into each cardinal direction, one meter apart. From these data, we
156 calculated the soil moisture at field capacity, using the functions of Saxton et al. (1986).
157
158 *Tree ring data and reconstruction of stand structure*
159
160 We glued the collected increment cores to core mounts and sanded to fine grit (600 for conifers,
161 1000 for deciduous). Owing to fragility of sample wedges from decayed dead trees, we immersed
162 some of the samples in white glue-solution (following Krusic & Hornbeck 1989, but in normal air
163 pressure), dried, and sanded. Less fragile wedges or sample discs we sanded similar to increment
164 cores. As absent rings can be common in these high-latitude forests (especially during years of poor
165 growth conditions), proper cross-dating is a pre-requisite for any annual resolution analyses using
166 tree ring data as it ensures that each year is assigned its exact year of formation. We cross-dated all
167 samples visually (2102 samples) and measured the tree ring widths using WinDendro software
168 (Regents Instruments Ltd., Canada) for easy samples, and a stereomicroscope with MeasureJ2X

169 software connected to a sliding stage (Velmex, Inc., USA) for difficult slow growing conifers and
170 for birch samples.
171
172 We based the reconstruction of the development of individual trees on the field data and tree ring
173 data. We back-calculated individual tree sizes by first taking the field-measured tree size as a
174 starting point. We then subtracted bark thickness (using species-specific bark thickness equations;
175 Ilvessalo 1965) and twice the width of the last ring (for diameter), to calculate diameter under bark
176 of the previous year. We then added bark thickness for the new diameter, and added it to this new
177 diameter. This way, we computed tree sizes (over bark) for each tree for each year. If a tree had
178 died during the reconstruction period, it was 'resurrected' at its cross-dated year of death. In years
179 preceding its death it was treated as a live tree and the change of its size was computed accordingly.
180 For downed dead trees the sampling height was sometimes higher than the 1.3 m height. In this
181 case, we relied on the pipe-model assumption that the area of each ring at the sampling height was
182 equal to the area of the same ring at 1.3 m height and converted that area to ring width at 1.3 m
183 height (beginning from the field-measured DBH, minus the bark).
184
185 We limited the analysis period to the last 50 years for conifers (1962-2011). From our earlier
186 experience there is a chance that some of the smaller *P. abies* that may have died early during the
187 reconstruction period have already decayed past the point where cross-dating their year of death is
188 possible, but as tree mortality events in these stands were quite rare, these errors should be small.
189 For *B. pubescens*, after an initial screening we limited the reconstruction period to the last 30-years
190 (1982-2011), as the *Epirrita*-outbreak in 1965-66 resulted in a large number of absent rings in the
191 data set for the trees that survived the outbreak.
192

193 *Climate and soil moisture variables*

194

195 For climate data, we used daily meteorological data generated using kriging interpolation of
196 national meteorological data (Venäläinen et al. 2005). The data are interpolated onto a 10 km × 10
197 km grid covering the whole of Finland, and we used the data from the grid point nearest to the
198 Värriö Subarctic Research Station (365 m a.s.l.). We converted the daily data to seasonal (winter =
199 DJF, spring = MAM, summer = JJA, fall = SON) temperature and precipitation variables. To
200 correct for temperature differences in elevation, we applied an adiabatic lapse rate of 0.6°C/100 m.
201 Other predictor variables tested included solar radiation, temperature sum and growing season
202 length. Solar radiation was obtained from Nöjd & Hari (2001). For calculating the temperature sum
203 we used a 5ºC threshold value.

204

205 In addition to these predictors, we used a daily water balance model, WATBAL (Starr 1999; Starr
206 & Alam 2015), to reconstruct seasonal soil moisture conditions. WATBAL is based on the model
207 by Bonan (1989), and is a capacity ("bucket") type model that calculates the water balance
208 components and changes in soil moisture available for plants at the end of each day. In addition to
209 climate data, the model takes into account soil characteristics of the site. Hence, the soil moisture
210 deficit values were calculated separately for each site (see Appendix S1 for detailed description).

211

212 We tested both current year and previous year variables in the growth modeling. To reduce the
213 number of predictor variables entering the growth model, we used common dendroclimatological
214 methods to screen for candidate climate variables, using correlation between species-specific mean
215 ring-width chronologies and climate variables (see Appendix S2). We entered variables that
216 explained a minimum of 5% of the variance in the ring-width indices into the model selection
217 procedure (below). For *P. sylvestris* these were: previous spring (MAM) temperature, current spring

and summer (JJA) mean temperature, previous and current year temperature sum, previous fall (SON) solar radiation, and previous fall precipitation amount. For *P. abies* these were: current summer mean temperature and solar radiation, current year temperature sum, and previous summer precipitation amount. In addition, based on findings from earlier studies (e.g., Mäkinen et al. 2000; Aakala & Kuuluvainen 2011), we also included current year winter temperatures. For *B. pubescens* the variables were: previous winter, summer and fall temperature, current summer temperature, previous and current year temperature sum, current year growing season length, and current summer precipitation amount.

WATBAL-modeled soil moisture values were used to calculate drought indices for each site and year: spring mean soil moisture content (current and previous year), summer mean soil moisture content (current and previous year), and fall mean soil moisture content (previous year) in the model selection procedure. We also tested minimum soil moisture values for the same seasons.

Tree-tree competition

To quantify the influence of tree-tree competition on tree growth we tested several variants of the neighborhood competition-index (NCI) proposed by (Canham et al. 2004). We modified the index so that all competitor species were treated equally, and the index was of the form:

$$\sum_{j=1}^{n} \frac{(DBH_j)^{\alpha}}{(distance_{ij})^{\beta}}$$

where DBH_j is the size of the competitor, and $distance_{ij}$ is the distance between the focal tree i and the neighboring tree j. Constants α and β determine the shapes of the effect of the competitor DBH and the distance to the competitor, on NCI. In selecting the exact variant of the competition index for the final modeling, we screened a number of candidate variants for different α and β, using a

similar procedure as that used by Hartmann et al. (2009). In this, we fit separate models for the exponents α and β (0.5, 1, 1.5, and 2.0). In the NCI trees are tallied within a circle of arbitrary size, or 'search radius'. We tested the effect of varying search radii, at 1 m intervals from 5 m to 8 m. We judged the performance of different exponents and radii, using Akaike's information criterion (AIC), with substantial differences in model fit indicated by a change in AIC values greater than two. This allowed us to assess which models, and hence predictors, were best supported by the data. Variant with the lowest AIC value was selected.

In this screening procedure, we used mean basal area increment of the most recent 20-years (1992-2011) as the response variable, and tree size in 1992 and the competition index as predictors. This initial screening for competition indices (*NCI*) was conducted using mixed effects modeling, with site as a random variable (random intercept). We made the assumption that the competition index that performs best in predicting the 20-year mean basal area increment is the most suitable also for the interannual analysis of growth. We used weighted edge correction (Getis & Franklin 1987), and chose 8 m as the maximum radius (approx. 1/4 of the side of the plot) to avoid unnecessarily large edge effects.

The best competition index (judged by the lowest AIC value) for all three species was when $\alpha = 0.5$ and $\beta = 1$ and the search radius was 5 m for *B. pubescens*, 7 m for *P. abies* and 8 m for *P. sylvestris*. It should be noted, however, that there were multiple variants of radius, α, and β within two ΔAIC units that is often considered as an indicator of meaningful differences in model performance, so the modeling approach was fairly insensitive to small changes in the parameter values (Appendix S3). In the final model, we calculated the competition index values separately for each year and for each tree, using these fixed values for radius, α, and β.

Modeling annual basal area increment

We modeled the annual variation in basal area increment of all trees that were alive in 2012 (although dead trees were included in the reconstruction of the competition index). We built separate models for each of the three species following the protocol of (Zuur et al. 2009). In short, after checking that collinearity of the predictor variables was not an issue, we started out with a full model with the following, annually varying candidate variables: log-transformed tree size, competition index and environmental variables (climate and soil moisture deficit), and static site-level variables soil field capacity, mean organic layer depth and elevation.

We determined the optimal random structure from among the models without random structure, site as random, tree as random, or tree nested within site as random. In all cases the random term was the intercept. As in the competition index selection, we used AIC to select the best model.

Due to the inherent autocorrelation present in tree ring width-derived data, we needed to account for the temporal autocorrelation to satisfy model assumptions of independence of errors. For this, we modeled the autocorrelation between residuals of different time points, using autoregressive-moving average (ARMA) models. We determined the optimal temporal correlation structure of residuals by testing several parameter variants of the ARMA-models. We limited the number of the autoregressive parameters to three and chose the variant based on AIC, and the visual analysis of model residuals as a function of time. Of the tested variants, we selected a third order autoregressive model with no moving average component. Adding more autoregressive parameters led to improvements in the AIC values, but the residuals were clearly positively biased.

We determined the optimal fixed component by fitting (maximum likelihood) the full model, testing for the significance of each term using likelihood ratio tests. Each time the least-significant term

was dropped, until all remaining terms were significant. We then fit the final models for each species, using restricted maximum likelihood, and validated the models through visual inspection of residuals (Zuur et al. 2009).

In assessing the model fits it became apparent that the models were unable to predict absent rings that we detected in some of the ring-width series during the cross-dating procedure. Assigning these absent rings unambiguously to specific calendar years was difficult, especially for *B. pubescens* which often has partial (wedging) rings that are possible even if the ring is otherwise wide. Thus trees that had more than 10% of rings absent during the modelling period were dropped (i.e., more than 5 missing rings for *P. sylvestris* and *P. abies*, and more than 3 missing rings for *B. pubescens*). Even after dropping these trees from the analyses, the absent rings greatly influenced the goodness-of-fit statistics and we report the results separately with both absent rings both included and omitted.

We also tested whether tree-tree competition influenced how trees respond to the environmental variables that were selected for the final models, by adding the interaction terms between competition and environmental variables. This procedure meant that only the environmental variables that were selected in the final models without interactions were tested. We added the interaction terms to the final models and dropped one interaction term at a time until all were significant. This selection procedure was also done with similar criterion, using likelihood ratio tests.

Models were fitted with original values and with standardized values (zero mean, unit standard deviation) for a rough comparison of the effect sizes of each predictor variable. We report here the standardized parameter estimates (parameter estimates with original values are in Appendix S4).

We assessed the goodness-of-fit for the final models, by computing the amount of variance in the measured basal area increment explained by the model predictions. Finally, to separate the influence of tree- and site-level variables (size, competition) from the environmental variables, we assessed drivers behind these trends by predicting growth, using 1) constant tree size, 2) constant neighborhood competition, and 3) constant tree size and competition (i.e. environmental variables only). All analyses were conducted in R (R Core Team 2016), and packages: dplR (Bunn et al. 2016),and nlme (Pinheiro et al. 2016).

Results

Model goodness-of-fit

Overall, the model fits varied among species. For *P. sylvestris* (32 090 tree rings, from 751 trees on 38 plots), the goodness-of-fit statistic (computed as the percentage of variance in the measured basal area increment explained by the fitted data, with site and tree-level random effect) was 49% (Fig. 2a). For *P. abies* (23 973 ring width measurements from 582 trees on 34 plots), the goodness-of-fit statistic value was 68% (Fig. 2b), and for *B. pubescens* (6881 ring width measurements from 232 trees on 37 plots), the value was 29% (Fig. 2c). For all species, model residuals were clearly larger for lower growth rates, i.e. high growth rates were predicted better than low growth rates (Fig. 3a-c).

It is noteworthy that these goodness-of-fit values and the spread of the residuals were greatly influenced by absent rings. When we excluded years with absent rings from the calculation of the goodness-of-fit, the value was 70% (*P. sylvestris*; 137 absent rings removed), 77% (*P. abies*; 28 absent rings), and 52% (*B. pubescens*, 92 absent rings), and the spread of residuals was more even (Fig. 3a-c).

Interannual variation

Of the characteristics of the individual *P. sylvestris*, tree size was the most important predictor of tree growth with a positive effect (Table 1). Competition (negative effect) and site elevation (positive effect) were also significant predictors. The effect of competition was clearly smaller than the positive influence of tree size or elevation. Of the seasonal environmental variables (climate variables and soil moisture), spring temperatures and temperature sums of the current and previous year were all significant predictors for growth of *P. sylvestris*, with a positive relationship. In contrast, summer soil moisture deficit of the current and the previous year had a consistent negative relationship with tree growth. Temperature sum had the strongest effect, but overall the influence of environmental variables was weaker than the influence of tree size.

Similar to *P. sylvestris*, size was the most important predictor of *P. abies* growth, with a positive effect on growth (Table 2). Competition and elevation were also important, and compared to *P. sylvestris*, the effect of competition was clearly stronger. Out of the environmental variables, winter temperatures and drought conditions in the previous summer and especially in the previous fall had a negative effect on growth, whereas summer temperature of the current year had a strong positive influence on growth.

For *B. pubescens* (Table 3), tree size and temperature sum had a positive influence on growth, similar to the two conifers. However, in contrast to the two conifers, soil moisture deficits in the spring and summer had a positive influence on *B. pubescens* growth.

Adding interaction terms between competition and environmental variables led to negligible improvements for *P. sylvestris* (AIC = 66 732 vs. 66 733 for models without interaction). Of the competition-environment interactions for *P. sylvestris*, summer soil moisture deficit and

368 competition had significant positive interaction, meaning that higher competition decreased the
369 negative influence of summer soil moisture deficit. For *P. abies*, none of the interaction terms were
370 significant.
371
372 *Growth trends*
373 On average, tree growth rates clearly increased during the period analyzed, for all three species.
374 This increase was the clearest for *P. sylvestris* (Fig. 4a) and *B. pubescens* (Fig 4c), but less evident
375 for *P. abies* (Fig. 4b). Slope of a linear regression model fitted to the time series of model
376 predictions was 2.09 mm^2yr^{-1} (CI: 1.95, 2.23) for *P. sylvestris*, 1.21 mm^2yr^{-1} (1.02, 1.41) for *P.*
377 *abies*, and 2.03 mm^2yr^{-1} (1.75, 2.31) for *B. pubescens*.
378
379 To separate the influence of tree and site-level variables from the environmental variables, we fitted
380 models where we held tree size, competition, and both size and competition constant and predicted
381 tree growth (Fig. 4a-c). We then compared the slopes of the fitted models to compare the strength of
382 each predictor as a determinant for growth rate change. For *P. sylvestris* (Fig. 4a), linear trend in
383 growth rate change over the 50-year interval dropped to 1.30 mm^2yr^{-1} (CI: 1.17, 1.42) when size
384 was held constant, increased slightly to 2.15 mm^2yr^{-1} (CI: 2.01, 2.30) when competition was held
385 constant. *P. sylvestris* model slope was 1.35 mm^2yr^{-1} when environmental variables alone were
386 included (CI: 1.22, 1.48) when both size and crowding were held constant.
387
388 For *P. abies* (Fig. 4b), the linear trend in growth change over the 50-year period was 0.19 mm^2yr^{-1}
389 (CI: 0.02, 0.36) when size was held constant, 1.28 mm^2yr^{-1} (CI: 1.08, 1.48) when competition was
390 held constant. When both size and competition were constant (i.e. environmental variables only),
391 the linear trend was 0.25 mm^2yr^{-1} (CI: 0.08, 0.42). For *B. pubescens* (Fig. 4c), the linear trend in the

full model was 2.03 mm^2yr^{-1} (CI: 1.75, 2.31), and when size was held constant 0.95 mm^2yr^{-1} (CI: 0.71, 1.19). Competition was not significant for *B. pubescens* and hence there was no third model. We note here that in the cases of both constant size and competition, the trend is the result of the environmental variables, as site-level variables (i.e., elevation in the final models for conifers) remain unchanged throughout the period, and random effects consist of intercepts only.

Discussion

We assessed tree growth trends, inter-annual variation and their drivers in three uneven-aged and unmanaged boreal forest landscapes in northern Finland. Unlike most empirical assessments in high latitude forests, our study was carried out using representative sampling of old-growth forests at the landscape level and included all main tree species, which is paramount for accurately depicting growth variations and trends (Nehrbass-Ahles et al. 2014). Based on analyses of national forest inventory data (a systematic sample over the entire country), Kauppi et al. (2014) and Henttonen et al. (2017) similarly found increasing tree growth rates in northern Finland. However, as their analyses included also managed forests, we have here demonstrated for the first time how tree growth has varied in this region in the absence of direct human influence.

In addition to the representative sampling in naturally developed forests, the inter-annual resolution in our analysis has additional benefits for understanding tree growth variation and its drivers. The annual reconstruction allows both an analysis on the changing competitive status (Weber et al. 2008), but also of the interactions between stand structure (competitive status of a tree) and climatic variability. This improves our understanding of how different tree species are likely to respond to changing climate and competitive states (Weber et al. 2008; Foster et al. 2016). However, it is worth pointing out that for analyzing tree ring data at an annual resolution, absent rings need to be properly handled through a rigorous cross-dating procedure.

Importantly, summer drought conditions had a small, but consistently negative influence on the growth of both *P. sylvestris* and *P. abies*. The role of droughts or precipitation is in general considered to be minor in these forests (Mikola 1956; Mäkinen et al. 2000), although it has been noted for *P. sylvestris* on dry sites (Kärenlampi 1972; Henttonen et al. 2014). However, in our analyses the drought limitations applied also to *P. abies*. As these two species differ in their niches regarding soil properties (Sutinen et al. 2002), our results demonstrated that drought may limit tree growth over a wide range of soil properties. The reason for these effects is likely related to our use of a water balance model parameterized for each study plot, hence leading to a physiologically more realistic representation of soil moisture conditions. This also implies that while the importance of accurate climate information for modeling tree growth is well-recognized (Foster et al. 2016), soil characteristics should also be considered. Taken together, the findings add to the growing body of literature on drought vulnerability in cool and mesic climates where droughts had not been previously considered problematic (Barber et al. 2000; Wilmking et al. 2004; Clark et al. 2016). For *B. pubescens* the soil moisture deficit was positive, and hence potentially an additional effect of temperature (cf. Ford et al. 2017).

Besides drought, other environmental variables that influenced tree growth were in line with earlier studies for trees in the northern boreal forests of Europe. Growing season temperature was generally the most important determinant as has been previously shown for all three species in northern Fennoscandian conditions (Henttonen 1990; Helama et al. 2002; Karlsson et al. 2004). Similarly, the negative relationship between *P. abies* growth and winter temperatures has been documented in earlier studies (Mäkinen et al. 2000; Aakala & Kuuluvainen 2011), and has been explained with the development and maintenance of winter hardiness in warm winters (Bradshaw et al. 2000).

442 Competition was a fairly modest driver of growth variation, when compared to tree size (effect sizes
443 in Tables 1-2), and it was not significant for *B. pubescens*. In general, competition is thought to play
444 a greater role as a growth determinant in more productive systems (e.g., Callaway 1998), so the
445 small influence of competition was expected in these high-latitude forests. Although at the stand-
446 level the canopy cover in these old-growth forests is sparse (which would suggest little competition
447 for light) the often-clustered spatial distribution of tree stems (Kreutz et al. 2015), means that
448 competition may still play a role (Fraver et al. 2014). Using the same trees as in the present study,
449 Aakala et al. (2016) showed that competition influenced crown asymmetry so that tree crowns
450 tended to expand away from their competitors, which is a competition-avoidance strategy and
451 probably an important explanation for the minor influence of competition on tree growth. That
452 competition was a stronger determinant for the shade-tolerant *P. abies* was also consistent with the
453 general notion that shade-tolerant tree species are most influenced by competitive interactions
454 (Kunstler et al. 2011). The finding that for *B. pubescens* competition did not enter the final models
455 is probably also related to the tendency for the species to reproduce from stump and root sprouts, so
456 competition belowground is perhaps not well expressed by a simple competition index.
457
458 A number of studies have demonstrated the interactions between competition and climate variables
459 (Bottero et al. 2017), but the mechanisms are still poorly understood (Grant et al. 2013; Thomas &
460 Waring 2015). In our analyses, only the summer soil moisture deficit for *P. sylvestris* interacted
461 with competition, and so that stronger tree-tree competition ameliorated the negative effects of
462 summer drought. This somewhat counter-intuitive result might be an expression of soil conditions
463 so that there are more (and/or larger) competitors (and hence higher competition index) on better
464 sites, which would mean that small-scale variation in edaphic conditions may have been an
465 explanation for the findings. All in all, we suspect that these findings are a result of the modest

influence of competition on growth in these forests in general, precluding the detection of any strong influences from competition on the growth-climate relationships.

When averaged over all trees, we found clearly increasing trends in tree growth in these landscapes. Positive trends were present for all three tree species, and most strikingly so for *B. pubescens*. In the models, the positive trends were to a large extent attributable to the increasing tree size, which is well-known to be a major determinant for tree growth rates (MacFarlane & Kobe 2006; Lapointe-Garant et al. 2010). However, attributing these types of changes in growth trends to specific drivers with statistical modeling is notoriously difficult (Brienen et al. 2017). They are confounded with covarying effects of other trend-like changes in the 20th century, such as the fertilization effects from the globally increasing CO_2 concentration, and spring warming, earlier snowmelt and N deposition that have been shown have occurred in the current study area or in the larger region (Hari et al. 2017; Irannezhad et al. 2017; Palviainen et al. 2017).

However, to examine the role of factors other than increasing tree size (i.e., environmental variables and competition) on these growth trends, we used the models to simulate tree growth with constant size, with constant competition, and with both size and competition held constant. The influence of competition was small, but for *P. sylvestris* and *B. pubescens*, growth trends were clearly positive even when only environmental variables were considered. For *P. abies*, growth trends were close to zero when tree size was held constant. Hence, although it was not possible reliably distinguish between different drivers behind the trends, the findings demonstrated clear species dependence in growth trends so that *P. sylvestris* and *B. pubescens* appeared to have benefited more from the environmental changes during the study period.

490 Positive trends in tree growth have been documented earlier in northern Finland, and in managed
491 forests, linked to climate change and forest management (Kauppi et al. 2014; Henttonen et al.
492 2017). However, for naturally developed forests, we speculate that there are two additional factors
493 that may have produced trends at the time scales analyzed here by keeping tree-tree competition
494 low in the past. First, the harsh growth conditions during the so-called Little Ice Age that ended in
495 the early 20th century has likely kept stand density low. The recovery from these conditions has
496 been suggested to have influenced forest structures in northern Sweden (Hofgaard 1993), and
497 increased the tree densities in the nearby treeline ecotone (Aakala et al. 2014). The second change
498 that has occurred is the almost-complete cessation of forest fires in the early 20th century that have
499 influenced particularly the *P. sylvestris*-dominated areas that tended to burn frequently as surface
500 fires (Aakala 2018). This explanation for the positive growth trends would also be consistent with
501 the observations of changing disturbance regimes influencing stand structures and succession
502 (Weber et al. 2008). It is likely that both, cold temperatures and frequent surface fires on drier sites
503 have kept the forests more open and hence tree-tree competition low. Supporting this, our data
504 showed an increase in the mean competition index value, by 15% from 1962 and 2011, indicating
505 that, on average, the recruitment and increasing neighbor sizes clearly surpassed the effect of tree
506 mortality. Hence, while the role of competition still remained limited, if stand development follows
507 a similar trajectory in the future it seems evident that the role of competition as a determinant of tree
508 growth will increase.
509
510 An additional explanation for any growth trends could be partial disturbances that relax the
511 competitive pressure on the surviving trees. For *B. pubescens*, the defoliator outbreak in mid-1960s
512 (Pulliainen 1976) had a large impact in reducing competition for survivors, and this, along with the
513 recovery from the defoliation in general probably explains a major part of the high, positive growth
514 trends for this species. However, except for one plot that had experienced a windthrow during the

study period, field observations suggested that no larger disturbances had occurred in the stands that could have been responsible for creating the observed growth trends, except for the earlier documented cessation of forest fires in the *P. sylvestris* dominated stands.

In addition to these variables, the growth of *P. sylvestris* and *P. abies* was influenced by site elevation. Elevation could be expected to influence growth due to its influence on temperature, but the influence here was positive, i.e. trees at higher elevation grew better than trees at lower elevations. It is evident that there was an unmeasured elevation-related covariate influencing growth in our study areas. We nevertheless wanted to keep it in the models, as it would otherwise be included in the site-level random effects for these species.

Conclusions

Old-growth forests at high latitudes have been considered stable systems, but our analyses showed that tree growth rates have been increasing in the past 50 years (30 years for *B. pubescens*) for all three main species. This growth increase was particularly apparent for *P. sylvestris* and *B. pubescens*, and may be partly explained by changing climate (end of the Little Ice Age, and 20th century spring warming) observed in this region, but potentially also by long-term changes in the disturbance regimes. Importantly, we found growth to decline during dry summers for both *P. abies* and *P. sylvestris*, and over a range of soil conditions. As was expected from a low productivity system, competition among trees had a minor influence on tree growth, but showed increases during the time period analyzed.

While tree growth at high latitudes in northern Europe is generally considered to be limited by temperature and hence to benefit from warming climate, the negative effects of drought on *P. sylvestris* and *P. abies*, and the negative effect of warm winters for *P. abies* suggest a complex

response to climate warming in the future. Combined with an increasing trend in the tree-tree competition means that the positive growth trends detected here are unlikely to continue in the future, and the response to warming climate will be species and site-dependent.

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Data accessibility: Growth data and time series of the independent variables are available at DOI: 10.6084/m9.figshare.7151945

Author contributions:

T.A. conceived of the research idea, collected the data with contributions from M.S., performed statistical analyses with contributions from F.B., and wrote the paper; M.S. computed the soil moisture deficits; all authors discussed the results and commented on the manuscript.

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702

703

704 **Supplementary material**

705 **Appendix S1.** Description of the water balance model WATBAL.

706 **Appendix S2.** Climate variable screening.

707 **Appendix S3.** Competition index selection.

708 **Appendix S4.** Non-standardized parameter estimates for the final models.

709

710 **Tables**

711

712 **Table 1.** Model summaries for *P. sylvestris*; *t* refers to current year variable, *t*-1 to previous year.
713 Separate models were fit with and without interactions (AIC = 66 733), competition × environment
714 (AIC = 66 732). Drought variables were computed, using the WATBAL model. Parameters φ_1, φ_2,
715 and φ_3 are the parameters of the third-order autoregressive model, used for modeling the temporal
716 autocorrelation of residuals. Random effects (tree within site) are given as standard deviations.

		Coefficiencts			
	Variable	No interaction		Compet. × environm.	
Fixed	Intercept	5.6032	***	5.6026	***
effects	Ln(size)	0.1791	***	0.1784	***
	Competition	-0.0718	**	-0.0732	**
	Elevation	0.2255	**	0.2254	**
	Spring T (t-1)	0.0307	***	0.0307	***
	Spring T (t)	0.0178	***	0.0179	***
	Temp. sum (t-1)	0.0319	***	0.0315	***
	Temp. sum (t)	0.0611	***	0.0615	***
	Summer drought (t-1)	-0.0256	***	-0.0149	***
	Summer drought (t)	-0.0151	***	-0.0285	***
	Competition×Summer drought (t-1)			0.0121	***
ARMA	φ_1	0.3476		0.3479	
	φ_2	0.1449		0.1447	
	φ_3	0.0940		0.0936	
Random	Site	0.2408		0.2401	
effects	Tree	0.5569		0.5572	
(SD)	Residual	0.7588		0.7586	

717 Notes:
718 Significance levels are n.s. - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

719

720

721 **Table 2.** Model summaries for *P. abies*; *t* refers to current year variable, *t*-1 to previous year.

722 Interaction terms were not significant and hence only the model without interactions is shown.

723 Notation otherwise similar to Table 1.

	Variable	Coefficiencts	
Fixed	Intercept	5.5879	n.s.
effects	Ln(size)	0.1757	***
	Competition	-0.1200	***
	Elevation	0.1421	*
	Summer T (t)	0.1165	***
	Winter T (t)	-0.0493	***
	Fall drought (t-1)	-0.0943	***
	Summer drought (t-1)	-0.0115	**
ARMA	φ_1	0.3702	
	φ_2	0.1017	
	φ_3	0.1360	
Random	Site	0.2648	
effects	Tree	0.5167	
(SD)	Residual	0.5145	

724 Notes:

725 Significance levels are n.s. - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

726

727 **Table 3.** Model summaries for *B. pubescens*; *t* refers to current year variable, *t*-1 to previous year.

728 Interaction terms were not significant and hence only the model without interactions is shown.

729 Notation otherwise similar to Table 1.

	Variable	Estimate	
Fixed	Intercept	4.9305	***
effects	Ln(size)	0.2383	***
	Temp. sum (t)	0.1061	***
	Spring drought (t)	0.0452	**
	Summer drought (t)	0.0585	**
ARMA	φ_1	0.2461	
	φ_2	-0.0022	
	φ_3	0.0861	
Random	Site	0.1855	
effects	Tree	0.6150	
(SD)	Residual	1.2179	

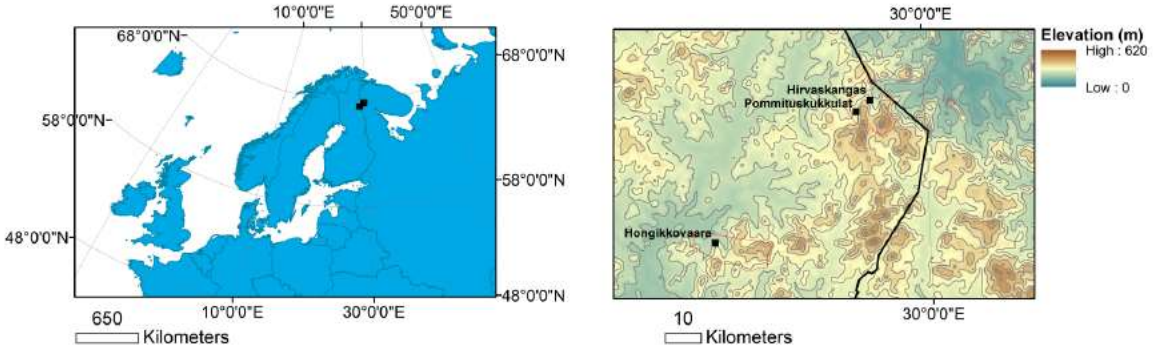
730 Notes:

731 Significance levels are $^{n.s.}$ - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

732

733

734 **Figures**

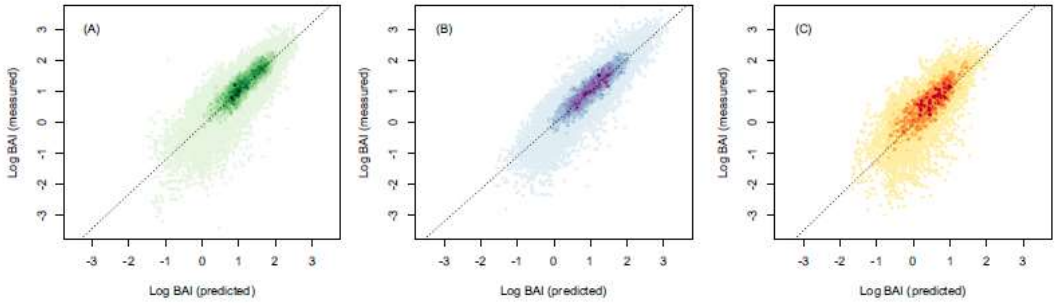


735

736 **Fig. 1.** Study landscape locations in the Värriö (Hirvaskangas and Pommituskukkulat) and Maltio

737 (Hongikkovaara) strict nature reserves, northern Finland.

738



739

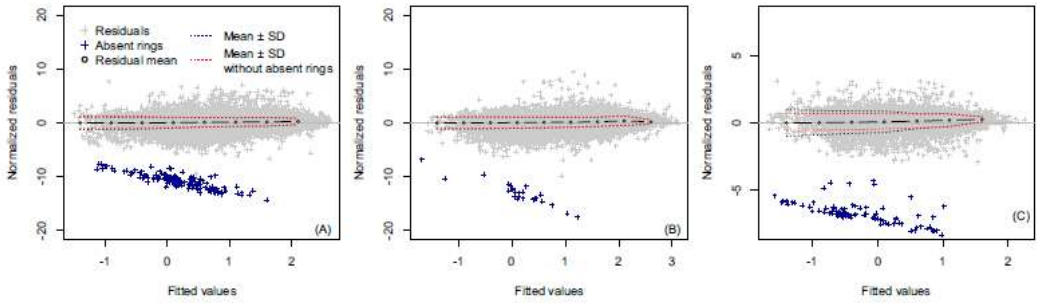
740 **Fig. 2.** Predicted vs. measured basal area increment for *P. sylvestris* (a), *P. abies* (b) and *B.*

741 *pubescens* (c), without absent rings. Color intensity describes the relative density of points, and the

742 dashed black lines a linear regression line between the fitted and measured basal area increments

743 (BAI).

744

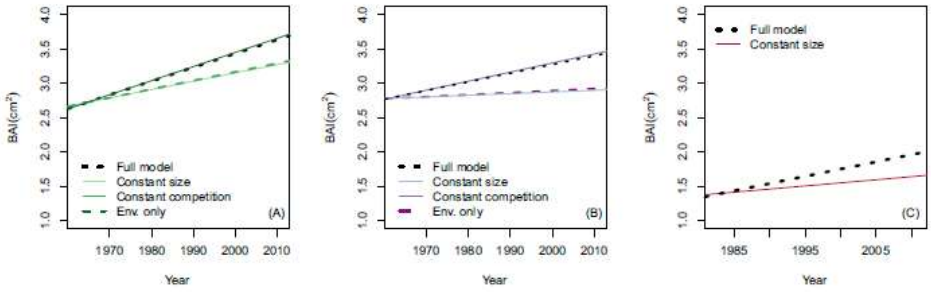


745

746 **Fig. 3.** The distribution of normalized residuals as a function of predicted values on a logarithmic
747 scale, for *P. sylvestris* (A), *P. abies* (B), and *B. pubescens* (C). Absent rings, and their influence on
748 the distribution of residuals are shown separately. .

749

750



751

752 **Fig. 4.** Linear regression models over the study period, when simulated using the full model,
753 constant tree size, constant competition and environment variables only, separately for the three
754 species *P. sylvestris* (a), *P. abies* (b), and *B. pubescens* (c).

755

Supporting Information to the paper Aakala, T., Berninger, F., and Starr, M. The roles of competition and climate in tree growth variation in northern boreal old-growth forests. *Journal of Vegetation Science*.

Appendix S1. WATBAL water balance model.

We used a daily water balance model, WATBAL (Starr 1999; Starr & Alam 2015; Abaker et al. 2017) to reconstruct seasonal soil moisture conditions over the study time period time period. WATBAL is based on the model by Bonan (1989), and is a capacity ("bucket") type model that calculates the water balance output components and changes in storage at the end of each day. The model is of the form

$$P = ET + R + D + \Delta SM + \Delta SOG \quad (1),$$

where, P= precipitation, ET= evapotranspiration, R= runoff (surface, shallow subsurface, and preferential flow), D = Drainage (percolation from the soil layer of interest), ΔSM= changes in soil moisture storage of soil layer of interest (typically the rooting zone), and ΔSOG = changes in the water equivalent of snow-on-ground (all units are in mm day^{-1}).

Evapotranspiration is calculated from a reference crop evapotranspiration (ET_o) value which is subsequently adjusted to a value for the forest stand (ET_c) using a crop coefficient approach (Allen et al. 1998) and then for the availability of soil water. ET_o is calculated using the Jensen-Haise alfalfa reference crop method (Jensen et al. 1990). Runoff in boreal forests can be expected to be restricted to the snowmelt period and in WATBAL is calculated as a fraction of the amount of water available for infiltration, i.e. positive values of rainfall plus snowmelt minus ET_c. The fraction of water available for infiltration depends on the type of soil parent material (till vs. sorted deposits) and its

texture (Soveri 1985). Snowmelt is calculated using a “temperature-index” method (Dingman 2002) in which the melt coefficient was calculated using the equation developed by Kuusisto (1980), based on the canopy cover fraction and air temperature. Drainage refers to water draining out of the soil layer by gravity, i.e. soil water in excess of field capacity. Soil moisture contents (SM) are calculated using as a piecewise linear function relating the actual to potential evapotranspiration ratio to the relative plant available water content of the soil (Zahner 1967; Dingman 2002). The plant available storage capacity of the soil is defined the difference in the water content of the soil when at field capacity and permanent wilting point. These soil hydraulic properties, as well as the water content of the soil at saturation, were calculated from soil texture data using the pedotransfer functions developed by Saxton and Rawls (2006), and assuming a constant organic matter content of 1%.

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Supporting Information to the paper Aakala, T., Berninger, F., and Starr, M. The roles of competition and climate in tree growth variation in northern boreal old-growth forests. *Journal of Vegetation Science*.

Appendix S2. Screening the climate variables.

Prior to mixed effects modeling, we screened for candidate variables to reduce the number of variables entering the model selection procedure. For this, we first created a mean value chronology for each species, following standard dendroclimatological procedures: we detrended each raw ring-width measurement series with a negative exponential function (Speer 2010), and prewhitened each series before computing a biweight robust mean value for each year. Chronologies were built, using R (R Core Team 2016), package dplR (Bunn et al. 2016).

We then computed correlations between the standardized ring-width indices and seasonal (DJF, MAM, JJA, SON) climate variables, separately for each of the three species (Tables 1, 2, and 3). Variables were tested for the current year, as well as the previous year. Variables, which explained minimum of 5% of variation in the ring-width chronologies were selected for further analyses. In addition, we included winter temperature for spruce, based on its significance in several earlier studies (Mäkinen et al. 2000; Aakala & Kuuluvainen 2011). In the screening procedure we used temperature measurements directly (i.e. without correcting for the adiabatic lapse rate) as the ring-width chronologies were constructed from all sites pooled.

Table 1. Variance in *Pinus sylvestris* ring width indices explained by seasonal climate variables. Variables that explained a minimum of 5% in variation in the ring width indices are in boldface.

Season	Variable	Year	Effect direction	R^2
winter	mean temperature	-1	+	0.04
spring	**mean temperature**	**-1**	**+**	**0.19**
summer	mean temperature	-1	+	0.02
fall	mean temperature	-1	+	0.01
winter	precipitation sum	-1	+	0.01
spring	precipitation sum	-1	+	0.02
summer	precipitation sum	-1	+	0
fall	**precipitation sum**	**-1**	**-**	**0.14**
spring	sunshine	-1	+	0.02
summer	sunshine	-1	+	0
fall	**sunshine**	**-1**	**+**	**0.05**
growing season	growing season length	-1	+	0.03
growing season	**temperature sum**	**-1**	**+**	**0.09**
winter	mean temperature	0	+	0.02
spring	**mean temperature**	**0**	**+**	**0.27**
summer	**mean temperature**	**0**	**+**	**0.1**
winter	precipitation sum	0	-	0
spring	precipitation sum	0	+	0.06
summer	precipitation sum	0	+	0
spring	sunshine	0	-	0.03
summer	sunshine	0	+	0
growing season	growing season length	0	+	0.02
growing season	**temperature sum**	**0**	**+**	**0.13**

Table 2. Variance in *Picea abies* ring width indices explained by seasonal climate variables. Variables that explained a minimum of 5% in variation in the ring width indices are in boldface.

season	variable	year	effect	r2
winter	mean temperature	-1	+	0
spring	mean temperature	-1	-	0
summer	mean temperature	-1	+	0.03
fall	mean temperature	-1	-	0.01
winter	precipitation sum	-1	-	0
spring	precipitation sum	-1	+	0
summer	**precipitation sum**	**-1**	**-**	**0.07**
fall	precipitation sum	-1	-	0.03
spring	sunshine	-1	-	0.01
summer	sunshine	-1	+	0.03
fall	sunshine	-1	+	0.01
growing season	growing season length	-1	-	0
growing season	temperature sum	-1	+	0.01
winter	mean temperature	0	-	0.03
spring	mean temperature	0	-	0
summer	**mean temperature**	**0**	**+**	**0.47**
winter	precipitation sum	0	-	0.04
spring	precipitation sum	0	-	0
summer	precipitation sum	0	+	0.01
spring	sunshine	0	-	0
summer	**sunshine**	**0**	**+**	**0.2**
growing season	growing season length	0	+	0
growing season	**temperature sum**	**0**	**+**	**0.31**

Table 3. Variance in *Betula pubescens* ring width indices explained by seasonal climate variables. Variables that explained a minimum of 5% in variation in the ring width indices are in boldface.

season	variable	year	effect	r2
winter	**mean temperature**	**-1**	**+**	**0.05**
spring	mean temperature	-1	-	0
summer	**mean temperature**	**-1**	**+**	**0.21**
fall	**mean temperature**	**-1**	**+**	**0.11**
winter	precipitation sum	-1	+	0.01
spring	precipitation sum	-1	+	0.01
summer	precipitation sum	-1	-	0
fall	precipitation sum	-1	+	0
spring	sunshine	-1	-	0
summer	sunshine	-1	-	0.02
fall	sunshine	-1	+	0.03
growing season	growing season length	-1	+	0.04
growing season	**temperature sum**	**-1**	**+**	**0.19**
winter	mean temperature	0	+	0.01
spring	mean temperature	0	+	0
summer	**mean temperature**	**0**	**+**	**0.18**
winter	precipitation sum	0	-	0
spring	precipitation sum	0	+	0.02
summer	**precipitation sum**	**0**	**+**	**0.06**
spring	sunshine	0	+	0.03
summer	sunshine	0	-	0
autumn	sunshine	0	-	0.03
growing season	**growing season length**	**0**	**+**	**0.14**
growing season	**temperature sum**	**0**	**+**	**0.26**

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Appendix S3. Screening for the competition index.

To quantify the influence of tree-tree competition on tree growth, we used the neighborhood competition-index proposed by Canham et al. (2004). The index requires that constants α and β, as well as a search radius for competing trees are carefully selected. Following the approach taken by Hartmann et al. (2009), we tested several variants for each of these constants: α and β were given values 0.5, 1, 1.5, and 2.0, and the search radius values were tested at 1m intervals from 5 m to 8 m.

In this screening procedure, we used 20-year mean basal-area increment as the response variable, and tree size and the competition index as the predictors. This initial screening for competition indices was conducted using mixed effects modeling, with site as a random variable, and was of the form:

$$\ln(BAI_{20}) = \ln(DBH) + \ln(NCI) + site + \varepsilon$$

We made the assumption that the relationship between tree growth and competition is static, i.e., the competition index that performs best in predicting the 20-year mean basal area increment is also the most suitable also for the interannual analysis of growth. We used weighted edge correction (Getis & Franklin 1987), and chose 8 m as the maximum radius (approx. 1/4 of the side of the plot) to avoid unnecessarily large edge effects. The indices with different variants α, β and radius were ranked, using the Akaike Information Criteria (AIC), separately for *P. sylvestris* (Table 1), *P. abies* (Table 2), and *B. pubescencs* (Table 3).

Table 1. Competition indices ranked for *P. sylvestris*.

Rank	Radius	α	β	AIC	ΔAIC
1	8	0.5	1	1741.742	0
2	7	0.5	0.5	1741.934	0.192
3	7	0.5	1	1741.993	0.251
4	6	0.5	0.5	1742.178	0.436
5	8	0.5	0.5	1742.254	0.512
6	8	1	1.5	1742.258	0.516
7	8	0.5	1.5	1742.259	0.517
8	7	1	1	1742.455	0.713
9	6	0.5	1	1742.477	0.735
10	8	1	2	1742.505	0.763
11	7	1	1.5	1742.519	0.777
12	7	0.5	1.5	1742.622	0.88
13	8	1	1	1742.646	0.904
14	7	1	0.5	1742.73	0.988
15	7	1	2	1742.931	1.189
16	8	1.5	2	1742.934	1.192
17	6	0.5	1.5	1743.043	1.301
18	7	1.5	1.5	1743.058	1.316
19	6	1	0.5	1743.093	1.351
20	7	1.5	2	1743.099	1.357
21	6	1	1	1743.121	1.379
22	7	1.5	1	1743.207	1.465
23	8	1.5	1.5	1743.207	1.465

24	8	0.5	2	1743.215	1.473
25	6	1	1.5	1743.3	1.558
26	7	0.5	2	1743.422	1.68
27	8	1	0.5	1743.503	1.761
28	7	1.5	0.5	1743.518	1.776
29	7	2	2	1743.563	1.821
30	6	1	2	1743.641	1.899
31	6	0.5	2	1743.658	1.916
32	7	2	1.5	1743.658	1.916
33	8	2	2	1743.712	1.97
34	8	1.5	1	1743.795	2.053
35	6	1.5	1	1743.854	2.112
36	7	2	1	1743.855	2.113
37	6	1.5	1.5	1743.875	2.133
38	6	1.5	0.5	1743.886	2.144
39	6	1.5	2	1743.959	2.217
40	8	2	1.5	1744.123	2.381
41	7	2	0.5	1744.146	2.404
42	5	0.5	2	1744.258	2.516
43	5	0.5	1.5	1744.265	2.523
44	6	2	1.5	1744.439	2.697
45	6	2	2	1744.44	2.698
46	6	2	1	1744.455	2.713
47	5	0.5	1	1744.464	2.722
48	6	2	0.5	1744.494	2.752
49	8	1.5	0.5	1744.544	2.802
50	8	2	1	1744.686	2.944
51	5	0.5	0.5	1744.787	3.045
52	8	2	0.5	1745.314	3.572
53	5	1	2	1745.489	3.747
54	5	1	1.5	1745.72	3.978
55	5	1	1	1745.973	4.231
56	5	1	0.5	1746.218	4.476
57	5	1.5	2	1746.551	4.809
58	5	1.5	1.5	1746.752	5.01
59	5	1.5	1	1746.941	5.199
60	5	1.5	0.5	1747.109	5.367
61	5	2	2	1747.309	5.567
62	5	2	1.5	1747.466	5.724
63	5	2	1	1747.607	5.865
64	5	2	0.5	1747.732	5.99

Table 2. Competition indices ranked for *P. abies*.

Rank	Radius	α	β	AIC	ΔAIC
1	7	0.5	1	1090.07	0
2	7	0.5	0.5	1090.37	0.3
3	7	0.5	1.5	1091.319	1.249
4	8	0.5	1	1092.442	2.372
5	8	0.5	1.5	1092.735	2.665
6	7	0.5	2	1093.228	3.158
7	8	0.5	0.5	1093.719	3.649
8	6	0.5	1.5	1093.901	3.831
9	8	0.5	2	1093.911	3.841
10	6	0.5	1	1093.913	3.843
11	7	1	1.5	1094.237	4.167
12	6	0.5	2	1094.595	4.525
13	7	1	2	1094.63	4.56
14	6	0.5	0.5	1094.702	4.632
15	7	1	1	1094.73	4.66
16	7	1	0.5	1095.651	5.581
17	8	1	2	1096.182	6.112
18	8	1	1.5	1096.269	6.199
19	5	0.5	2	1096.371	6.301
20	7	1.5	2	1096.475	6.405
21	5	0.5	1.5	1096.774	6.704
22	7	1.5	1.5	1096.972	6.902
23	6	1	2	1097.018	6.948
24	8	1	1	1097.231	7.161
25	6	1	1.5	1097.312	7.242
26	5	0.5	1	1097.656	7.586
27	7	1.5	1	1097.764	7.694
28	6	1	1	1097.983	7.913
29	7	2	2	1098.266	8.196
30	8	1.5	2	1098.382	8.312
31	7	1.5	0.5	1098.494	8.424
32	8	1	0.5	1098.53	8.46
33	6	1	0.5	1098.706	8.636
34	5	0.5	0.5	1098.731	8.661
35	7	2	1.5	1098.919	8.849
36	6	1.5	2	1098.954	8.884
37	8	1.5	1.5	1099.18	9.11
38	5	1	2	1099.41	9.34
39	6	1.5	1.5	1099.546	9.476
40	7	2	1	1099.604	9.534
41	5	1	1.5	1100.059	9.989
42	7	2	0.5	1100.14	10.07

43	6	1.5	1	1100.188	10.118
44	8	1.5	1	1100.218	10.148
45	8	2	2	1100.33	10.26
46	6	2	2	1100.437	10.367
47	6	1.5	0.5	1100.712	10.642
48	5	1	1	1100.793	10.723
49	6	2	1.5	1101.004	10.934
50	8	1.5	0.5	1101.088	11.018
51	8	2	1.5	1101.177	11.107
52	5	1.5	2	1101.299	11.229
53	5	1	0.5	1101.43	11.36
54	6	2	1	1101.522	11.452
55	5	1.5	1.5	1101.873	11.803
56	6	2	0.5	1101.909	11.839
57	8	2	1	1101.976	11.906
58	5	1.5	1	1102.405	12.335
59	8	2	0.5	1102.546	12.476
60	5	2	2	1102.561	12.491
61	5	1.5	0.5	1102.821	12.751
62	5	2	1.5	1103.016	12.946
63	5	2	1	1103.409	13.339
64	5	2	0.5	1103.705	13.635

Table 3. Competition indices ranked for Betula pubescens.

Rank	radius	α	β	AIC	ΔAIC
1	5	0.5	1	481.645	0
2	5	0.5	0.5	482.531	0.886
3	6	0.5	1	482.916	1.271
4	5	0.5	1.5	483.246	1.601
5	8	0.5	1	484.003	2.358
6	6	0.5	1.5	484.062	2.417
7	8	0.5	1.5	484.589	2.944
8	6	0.5	0.5	484.608	2.963
9	7	0.5	1	485.077	3.432
10	5	1	1.5	485.112	3.467
11	6	1	1.5	485.174	3.529
12	7	0.5	1.5	485.177	3.532
13	5	1	2	485.56	3.915
14	6	1	2	485.577	3.932
15	5	1	1	485.586	3.941
16	6	1	1	486.1	4.455
17	5	0.5	2	486.236	4.591

18	8	0.5	0.5	486.706	5.061
19	5	1	0.5	486.759	5.114
20	6	0.5	2	486.771	5.126
21	8	1	2	486.852	5.207
22	8	1	1.5	486.901	5.256
23	6	1.5	2	486.958	5.313
24	8	0.5	2	487.053	5.408
25	7	0.5	2	487.237	5.592
26	5	1.5	2	487.304	5.659
27	6	1.5	1.5	487.529	5.884
28	7	1	2	487.535	5.89
29	5	1.5	1.5	487.583	5.938
30	7	0.5	0.5	487.767	6.122
31	7	1	1.5	487.942	6.297
32	6	1	0.5	487.97	6.325
33	5	1.5	1	488.235	6.59
34	8	1	1	488.528	6.883
35	6	2	2	488.605	6.96
36	6	1.5	1	488.718	7.073
37	5	2	2	488.894	7.249
38	8	1.5	2	488.947	7.302
39	5	1.5	0.5	489.102	7.457
40	5	2	1.5	489.299	7.654
41	6	2	1.5	489.397	7.752
42	7	1	1	489.612	7.967
43	5	2	1	489.881	8.236
44	7	1.5	2	489.944	8.299
45	8	1.5	1.5	489.997	8.352
46	6	1.5	0.5	490.162	8.517
47	6	2	1	490.489	8.844
48	5	2	0.5	490.537	8.892
49	8	1	0.5	490.98	9.335
50	7	1.5	1.5	491.048	9.403
51	8	2	2	491.07	9.425
52	6	2	0.5	491.618	9.973
53	8	1.5	1	491.716	10.071
54	7	1	0.5	491.839	10.194
55	7	2	2	492.071	10.426
56	8	2	1.5	492.281	10.636
57	7	1.5	1	492.597	10.952
58	7	2	1.5	493.177	11.532
59	8	1.5	0.5	493.413	11.768
60	8	2	1	493.702	12.057

61	7	1.5	0.5	494.1	12.455
62	7	2	1	494.414	12.769
63	8	2	0.5	494.892	13.247
64	7	2	0.5	495.479	13.834

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Appendix S4. Model summaries for models without standardization.

Table 1. Model summaries for *Pinus sylvestris*; *t* refers to current year variable, *t*-1 to previous year.

		No interaction		Compet. × environm.	
	Variable	Estimate		Estimate	
Fixed effects	Intercept	-0.0118	n.s.	-0.2594	***
	Ln(size)	0.4573	***	0.4654	***
	Competition	-0.0002	**	0.0004	n.s.
	Elevation	0.0069	***	0.0069	***
	Spring T (t-1)	0.0231	***	0.0230	***
	Spring T (t)	0.0130	***	0.0130	***
	Temp. sum (t-1)	0.2630	***	0.2591	***
	Temp. sum (t)	0.4903	***	0.4927	***
	Summer drought (t-1)	-0.0043	***	-0.0025	***
	Summer drought (t)	-0.0025	***	-0.0074	***
	Competition×Summer drought (t-1)			0.0000	**
ARMA	φ_1	0.3477		0.3479	
	φ_2	0.1450		0.1449	
	φ_3	0.0941		0.0937	
Random effects (SD)	Site	0.2440		0.2436	
	Tree	0.5560		0.5563	
	Residual	0.7590		0.7589	

Notes:
Significance levels are $^{n.s.}$ - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$. Temperature sum is re-scaled (divided by 1000) for a more informative parameter value

Table 2. Model summaries for *Picea abies*; *t* refers to current year variable, *t*-1 to previous year.

	Variable	Estimate	
Fixed effects	Intercept	-0.0390	n.s.
	Ln(size)	0.4747	***
	Competition	-0.0004	***
	Elevation	0.0056	*
	Summer T (t)	0.0983	***
	Winter T (t)	-0.0224	***
	Fall drought (t-1)	-0.0051	***
	Summer drought (t-1)	-0.0007	**
ARMA	φ_1	0.3702	
	φ_2	0.1017	
	φ_3	0.1360	
Random effects (SD)	Site	0.2648	
	Tree	0.5167	
	Residual	0.5145	

Notes:
Significance levels are $^{n.s.}$ - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$. Temperature sum is re-scaled (divided by 1000) for a more informative parameter value

Table 3. Model summaries for *Betula pubescens*; *t* refers to current year variable, *t*-1 to previous year.

	Variable	Estimate	
Fixed effects	Intercept	1.1281	n.s.
	Ln(size)	0.7250	***
	Temp. sum (t)	0.0093	***
	Spring drought (t)	0.0018	**
	Summer drought (t)	0.0477	**
ARMA	φ_1	0.2460	
	φ_2	-0.0022	
	φ_3	0.0861	
Random effects (SD)	Site	0.1855	
	Tree	0.6150	
	Residual	1.2179	

Notes:

Significance levels are $^{n.s.}$ - $p > 0.05$, * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$. Temperature sum is re-scaled (divided by 1000) for a more informative parameter value